Inter-specific comparative analysis of distribution and habitat use patterns of benthic decapod crustaceans in shallow waters

A. Pallas[1], B. García-Calvo[1], A. Corgos[1], C. Bernárdez[2], J. Freire[1]*

[1]Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de A Coruña, Campus de A Zapateira s/n, A Coruña 15071, Spain

[2]Centro de Ecología Costera, Centro Universitario de la Costa Sur, Universidad de Guadalajara, V. Gómez Farias 82, San Patricio-Melaque, Jalisco 48980, Mexico

*email: jfreire@udc.es

ABSTRACT: Coastal areas have been widely considered as nurseries for many marine species. New approaches to this concept take into account interactions among environmental variables and ecological variations related to geographical location, as well as complex life cycles of marine invertebrates. We present a comparative approach to assess the relevance of environmental variables on the determination of patterns of distribution and habitat use of benthic decapod species in coastal areas. We hypothesize that this approach allows us to infer processes originating these patterns and to identify the main habitat use models. An intensive fine-grain sampling design was used to take into account the environmental gradients occurring at different spatial scales (defined by substrate type, depth, exposure and geographical location) in a temperate oceanic bay (Ria de A Coruña, Spain). A high proportion of juveniles were found in most populations, but the results do not allow us to generalize the idea of coastal areas as potential nurseries, except for few species with a marked spatial segregation between juveniles and adults. Larval transport seems to be the main process regulating mesoscale distribution patterns, while microscale distribution responds to a complex interaction among different processes, i. e. habitat selection at settlement, differential mortality among habitats, post-settlement dispersal and ontogenetic habitat shifts. Sandy substrates showed low-diversity communities dominated by hermit crabs. In rocky bottoms, variability in spatial patterns was mostly related to substrate type and geographical location. Caridean shrimps showed higher densities on flat rock surfaces, with similar juvenile and adult patterns. Anomuran

species occurred mainly on cobbles. Distribution patterns of brachyurans varied among species, but did not change greatly from juveniles to adults.

KEY WORDS: Spatial scale; Nursery habitat; Habitat selection; Settlement; Decapod crustaceans; Coastal ecosystems; Habitat use; Distribution; Ria de A Coruña

INTRODUCTION

Coastal areas are widely considered as nursery habitats for a high number of marine vertebrate and invertebrate species. Traditionally, nursery habitats have been defined as areas where juveniles occur at higher densities, avoid predation more successfully or grow faster than in other habitats (see review in Gillanders et al. 2003). Beck et al (2001) proposed a more accurate definition which includes the relative contribution of each potential nursery habitat to the adult population. Furthermore, new approaches apply this concept not to an entire area, but to a specific habitat defined by the complex interaction of environmental variables and ecological functions related to local variations (Beck et al. 2001, Stoner 2003). In addition, this concept has been so far studied mainly for a few fish and invertebrate species and for a limited number of ecosystem types (e.g. mangroves, coral reefs, estuaries) (Beck et al. 2001, Gillanders et al. 2003). Population dynamics of benthic invertebrates shows great differences from that of fish, and is determined mainly by complex life cycles, with pelagic phases which carry out medium or large-scale dispersion, and benthic phases characterised by a limited mobility respect to fish (Roughgarden et al. 1988). These differences, along with the high diversity of coastal habitats which so far have been poorly studied, suggest the need of further studies in order to produce general hypotheses and theories about mechanisms of population regulation in coastal ecosystems.

Shallow benthic habitats are structurally complex environments where a high number of biotic and abiotic factors (such as predation or physical disturbance, respectively) determine habitat quality and generate different stress levels that determine population and community structure and dynamics. These factors act at different spatial scales, creating gradients that can occur in the order of meters (microscale), 100s meters or

kilometres (mesoscale) or even in the order of 10s-100s kilometres (macroscale) (Orensanz & Jamieson 1998). As a response to this variability, benthic organisms might select their habitat in order to minimize the trade-offs among different stress factors.

The process of habitat selection could occur in two phases of the life cycle. Firstly, most benthic invertebrates can show a certain level of active selection at larval settlement and metamorphosis (Paula et al. 2001, Van Montfrans et al. 2003) and early benthic stages (Moksnes et al. 2003); this selection is probably aimed to avoid high levels of mortality commonly associated to this critical moment in their life cycle. Complementarily, differential mortality among habitats also contributes to determine the final distribution patterns of juveniles (Palma et al. 1999, Robinson & Tully 2000).

Mobile invertebrates could also modify their habitat preferences in later benthic stages, either by carrying out ontogenetic habitat shifts in certain phases of their life cycle (Pile et al. 1996, Moksnes 2004) or by showing a differential habitat use related to different behaviours (e.g. foraging, mating, etc).

Decapod crustaceans are a suitable group to be used as a model for studying the interplay of recruitment processes, habitat selection and postlarval mortality, due to their mobility, complex life cycles and population dynamics. Decapod crustaceans play a relevant ecological role in the dynamics of coastal benthic ecosystems, due to their high abundance in these areas and high taxonomic and trophic diversity (Squires 1990, Ingle 1996, Freire et al. submitted). Many species of this group are also economically important since they support outstanding fisheries, most of them in coastal areas (Caddy 1989, Squires 1990, Freire et al. 2002).

In the present study we apply a comparative approach to analyze patterns of distribution and habitat use of different decapod species inhabiting coastal areas. We hypothesize that this approach will allow us to infer habitat-related differences in population-level processes from the observed distribution and abundance patterns. An intensive sampling using a fine-grain spatial design was used to take into account the different environmental gradients occurring in a coastal ecosystem at different spatial

scales. By employing this methodology we will try to assess whether the studied habitats or a subset of them constitute potential nurseries for some benthic decapod species. In addition, the hierarchical relevance of different environmental variables on the processes determining spatial distribution and habitat use of decapod species will be analysed.

MATERIALS AND METHODS

Sampling. A stratified random sampling was carried out along the coast of the Ria de A Coruña in July and August 1998 (Figure 1). Previous studies suggested that in temperate latitudes a settlement peak takes place during these months for many invertebrate species (Pfister 1997). The study area is a coastal embayment located in the north-western Iberian Peninsula. Its main axis is 5 km long and has a north-south orientation; the mean depth is 25 m in the outer zones and 10 m in the inner part (Cosme de Avilés & Prego 1995). Three sites along the eastern coastline of the Ria were selected to sample the meso-scale variability (sites were separated by 1.5-2.5 km). The western coastline has been subject to a high urban development and was not included in this study.

An array of sampling locations was defined within each site according to the combination of three micro-scale variables:

- Wave exposure: exposed and sheltered locations (separated by 100s m) were selected depending on their orientation respect to the mouth of the bay. Seaweed communities were also observed to confirm the exposure level assigned to each location.
- Depth, using three nominal strata: 0 (low intertidal), 1 (3-5 m) and 2 (8-12 m). Depths are indicated in relation to Lowest Low Water. Locations at different depths within the same site and exposure were separated among them by 10s m.
- Substrate type. Four types of relevant substrates were identified in the study area: sandy bottoms, flat rock surfaces covered with small seaweeds, cobbles

and boulders, and kelp (*Saccorhiza polyschides*) holdfasts. Distances among sampled substrates in a given depth were in the order of a few meters.

Every possible combination of factor levels (site, exposure, depth and substrate) was sampled, with two exceptions. Wave exposure was always considered as sheltered for samples taken at depth 2, assuming that the importance of the effect of the waves is significantly reduced under 8 m deep. Sandy bottoms appeared only in significant proportions in the most internal site and thus they were sampled only there.

A suction sampler operated by scuba divers was used. This device consisted of a PVC pipe (length 1.70 m, inner diameter 7.5 cm) provided with an air diffuser connected to an air compressor and fitted to a 0.5 mm mesh-size bag. Rock surfaces, cobbles and sandy bottom samples were taken by placing 50x50 cm stainless steel quadrats on the substrate and suctioning the epibenthos. Different operations were employed in every substrate type. Flat rock surfaces were previously scraped to separate algae and sessile organisms, which were suctioned. Cobbles and boulders <7.5 cm diameter were suctioned, as well as the underlying sediment; larger cobbles were scraped and sessile organisms were suctioned. Sandy bottoms were suctioned to 5 cm deep. Each kelp holdfast was considered a sample and was randomly chosen and pulled up manually before suctioning its content. Four replicate samples were taken in each location.

Samples were washed and transferred to plastic bags for freezing at -20ºC. After defrosting, decapod crustaceans were separated, fixed in a dissolution of 4% formaldehyde in seawater and subsequently conserved in 70% ethanol. Specimens were identified following the taxonomical keys of Hayward & Ryland (1995) and González-Gurriarán & Méndez (1986). The following biological data were recorded: sex, presence of brood in females, and body size measured as carapace length in Caridea and Paguridea, and as major carapace axis in Brachyura and other Anomura (carapace width in all taxa except Majids and *Galathea strigosa*). Carapace length excluded the rostrum except for *Inachus phalangium* and *Macropodia rostrata*. Morphometrical measurements were taken using a stereoscopic microscope for individuals <20 mm and a calliper for larger specimens.

Most individuals were identified at the species level, except in some cases due to the taxonomical difficulties, especially in juvenile phases. Species of the superfamily Paguridea show allometric growth of the characters used in taxonomy (Benvenuto & Gherardi, 2001; Bertini & Fransozo, 1999), difficulting the identification of early stages; due to the high proportion of newly settled juveniles found, these species were pooled as a single taxon. Some genera (*Eualus, Hippoyte, Palaemon, Processa, Pilumnus* and *Xantho*) were represented in the collected samples by two species, and differentiation between them was impossible for a high proportion of damaged or early stage specimens; thus, these species were pooled as genera for data analyses.

Size at onset of maturity was used to estimate the abundance and relative proportions of juveniles and adults in the samples for each taxon (Table 1). Maturity size was estimated according to the following criteria: I) size of the smallest ovigerous female found (excluding outliers) and II) maturity size reported in literature. In the case of *Ebalia tuberosa*, no information about size at maturity was available and the maturity size of the two individuals found was not determined. Criterium I was only used when the number of ovigerous females was large (>15 individuals) or when no information about maturity size of the species was available in the literature. When identification to species level was not possible, the minimum size at maturity estimated for the taxon was applied (Zariquiey Alvarez 1968, Williams 1984, Hayward & Ryland 1995, Oh & Hartnoll 1999, Squires et al. 2000, Marine Information Network for Britain & Ireland: http://www.marlin.ac.uk/baski/baski_sp_home.htm, Crustikon, University of Tromso: http://www.tmu.uit.no/crustikon/Decapoda/Decapoda2/Species_index.htm).

Data analysis. The most abundant taxa (those that constituted more than 1% of the total abundance) were included in data analyses. Mean densities of each species were calculated as number of individuals$\cdot m^{-2}$ for cobbles, flat rock surfaces and sandy bottom substrates; since this was not possible for kelp holdfast samples, densities were calculated as number of individuals per holdfast.

Generalized linear models (GLM) were employed to determine the quantitative effect of the environmental conditions (related to site, exposure, depth and substrate) on the spatial patterns of the postlarval populations. The best subsets procedure using the Akaike Information Criterion (AIC) was used to select the best model, and a normal error and log link were assumed. Juvenile and adult abundances were analysed using GLMs. Due to the different density units used for holdfast and the rest of samples, analyses were performed separately for this habitat. Sandy bottom samples were also excluded from the GLM models given the completely different specific composition and structure of the communities found and the absence of this habitat at the two most external sites. Statistical models for rocky bottoms were fitted both for the complete data set and for flat rock surfaces and cobbles separately.

RESULTS

A total of 8843 individuals were found in the samples. 34 species were represented, as well as the superfamily Paguridea which was not identified to species level. The size frequency distribution of each infraorder showed a pronounced dominance of smaller size classes, indicating a high proportion of first juvenile instars (Fig. 2).

Juveniles of all taxa were found in the sampled area, whereas in two taxa (*Palaemon* spp., *Galathea strigosa*) adults were absent. The proportion of adults was low (32%) in all the studied habitats and for almost all species, with the exception of *Thoralus cranchii*, for which adults were more abundant than juveniles in all habitats (70%). Species of the superfamily *Paguridea* also showed a higher proportion of adults (63%) than of juveniles in all the rocky bottom habitats (Table 1).

Sandy substrate. Sandy and rocky bottom samples showed clearly different assemblages. Sandy substrate showed an extremely low specific diversity, dominated by species of the superfamily *Paguridea* (families *Paguridae* and *Diogenidae*). Pagurids reached very high densities (up to 1227 individuals/m^2 in deepest areas) and populations were composed almost exclusively by newly settled individuals, under 2

mm carapace length (98.1%). Other species appeared occasionally in very low densities (Fig. 3).

Rocky subatrates. Although all the tested variables showed an important effect on the distribution of decapod species, variability in spatial patterns for most taxa is mainly related to two variables: substrate type and sampling site (Table 2). Effects of depth and wave exposure on spatial distribution of postlarvae were quantitatively lower.

Similar patterns regarding parameters included in GLM were found in juveniles and adults on rocky bottoms (Table 2). In both cases substrate type was included in most of the models (85% for juveniles, 73% for adults), while wave exposure showed the lowest percentage of occurrence in models for both juveniles (62%) and adults (45%). However, sampling site was also included in the same proportion of models as substrate type for juveniles.

For most species, the proportion of adults was lower at deeper zones and juveniles showed higher densities at the external sampling site, with only one clear exception in *Athanas nitescens*, which occurred mainly in the internal site (Fig. 3). Spatial differences in distribution were generally more pronounced for juveniles than for adults, which were more evenly distributed among the different habitats. Differences in adult and juvenile proportion also showed the existence of different habitat use in juvenile and adult stages for some species, mainly regarding wave exposure and depth.

Attending to each infraorder independently, we found that caridean shrimps showed higher densities on flat rock surfaces, except for *A. nitescens* and *Eualus* spp. which occurred also on cobbles in high densities (Fig. 4). Vertical distribution of juveniles varied among species, occurring from low intertidal (genera *Palaemon* and *Processa*) to 8-10 m (*Athanas nitescens*, *Eualus* spp. and *Hippolyte* spp.). Although differences due to exposure level were not significant according to GLM, most caridean juveniles occurred preferently (*A. nitescens*, *Processa* spp.) or exclusively (*Eualus* spp.) in sheltered zones, but *Thoralus cranchii* was more abundant in exposed areas.

In most carideans, adult distributions followed similar patterns to those of juveniles, although densities were generally lower. However, differences among habitats in adult densities were less pronounced and their distribution range was wider, especially regarding exposure level and depth (*A. nitescens*), and in some cases differences among habitats were not significant (*Processa* spp.). Some of the taxa also disperse to internal sites (genera *Eualus* and *Hyppolite*). *Thoralus cranchii* adults appeared in higher densities than juveniles in all habitats and showed similar distribution patterns (Fig. 4).

The distribution of brachyuran juveniles was mainly determined by substrate type, although with variable patterns among species. *Pilumnus* spp. and *Pirimela denticulata* occurred almost exclusively on flat rock surfaces, while *Xantho* spp. appeared mostly on cobbles. These patterns were consistent in adults for *Pilumnus* and *Xantho*, although in this last genus a different vertical distribution pattern was observed, with juveniles located in deeper areas and adults in the low intertidal. Densities observed for adults of *P. denticulata* were very low (<0.30 ind/m^2) in all habitats (Fig. 5). Many other brachyuran species were found in low densities (<1% of total abundance) and therefore were not included in the statistical analyses; in many of these species adults were absent.

Anomuran species like *Pisidia longicornis, Porcellana platycheles* and *Galathea strigosa* showed clear habitat preferences, occurring mainly or exclusively on cobbles at medium and higher depths. *P. longicornis* maintained a similar distribution during all their life cycle, although a slight dispersion of adults towards intertidal zones was observed. *P. platycheles* showed a differential vertical distribution of different maturity stages, with a higher proportion of adults at intertidal zones. No adults of *G. strigosa* were found. Regarding exposure level, *G. strigosa* and *P. longicornis* were mainly found in exposed areas, whereas *P. platycheles* occurred only in sheltered habitats. On the other hand, the *Paguridea* were mainly represented by adult stages in rocky habitats, although juveniles found showed clear habitat preferences which were less distinct in adult phases (Fig. 5).

Kelp holdfasts. Almost all taxa found in rocky bottoms occurred also in kelp holdfasts, except in the case of the genus *Eualus*. The GLM results for kelp holdfast samples showed a lower effect of all the factors on juvenile and adult patterns compared to the results obtained in rocky samples, with no relevant differences among variables. 50% of the models obtained for juveniles and 33% of those for adults were not significant ($p>0.05$) (Table 3).

Distribution in holdfasts for most species followed the same patterns as in rocky bottoms regarding sampling site, depth and exposure level. However, it is remarkable that species like *G. strigosa, P. platycheles, A. nitescens and Xantho spp.*, which appeared mostly or exclusively on cobbles, occurred only in kelp holdfasts located in sheltered zones. Juveniles of *G. strigosa* appeared in relatively high densities in hodlfasts (up to 2.5 individuals per holdfast), although they could not be compared directly to densities in rocky samples.

Mean total densities in kelp holdfasts were 14.1 ind. per holdfast for juveniles and 8.9 ind. per holdfast for adults. Generally, proportion of adults of each species were equal (*T. cranchii, Pilumnus* spp*., P. longicornis*) or higher (*A. nitescens, Hyppolite* spp.) than in rocky bottom samples, with cases like the genus *Xantho* where the proportion of adults reached 92% in holdfasts. The few species in which only juveniles appeared (*Palaemon* spp. and *P. platycheles*) showed very low densities in holdfasts.

DISCUSSION

Potential nursery role of shallow habitats

The higher proportion of juveniles found for most species suggests that the sampled areas are juvenile habitats. Nevertheless our results do not allow us to consider the area as a general nursery for decapods, according to Beck et al. (2001), since some of the premises they establish are not fulfilled for all species. First, the high juvenile densities found may be explained not only by the potential nursery role of these

habitats but also by the high levels of larval settlement taking place during summer in temperate latitudes (Pfister 1997).

On the other hand, the nursery role concept is only applicable to life history strategies where there is a disjunction between juvenile and adult habitats. Some species (e.g. *Porcellana platycheles*, *Pisidia longicornis, Pilumnus* spp.) lacked a spatial segregation between juvenile and adult phases at the studied scales. Other species (e.g. *Athanas nitescens*, *Eualus* spp., *Xantho* spp.) seem to have a certain spatial segregation, with juveniles occurring in a subset of adult habitats. However, the ontogenetic changes in distribution seem to respond to dispersion, which could be due to density-dependent factors and to a wider stress tolerance range rather than to changes in habitat requirements (see Moksnes 2004). Adults of *Palaemon* shrimps were not found, but their high mobility may allow them to easily avoid the sampling device, thus their absence in the samples does not imply habitat segregation.

For *Galathea strigosa* only juveniles were present, as well as for some low-density brachyurans excluded from data analyses (e.g. *Cancer pagurus*, *Maja brachydactila*). Since there is evidence of adult presence at higher depths (Hayward et al. 1995, Fariña et al. 1997, Freire et al. 2002, Gonzalez-Gurriaran et al. 2002), we hypothesize that these shallow habitats may play an important nursery role for these species. However, the absence of adults in these areas does not imply their migration to other areas. The differential ontogenetic distribution found in pagurids also suggests a settlement function and a potential nursery role of sandy bottoms for this group. Further studies must test these hypotheses taking into account the juvenile survival, growth and movement to adult habitats (see Beck et al. 2001, Gillanders et al. 2003).

Finally, the results obtained in *Thoralus cranchii*, in which adults were more abundant than juveniles, might be due to inter-cohort variability in recruitment, since no spatial segregation was observed.

Effects of environmental variables on distribution patterns

The strong mesoscale variation on the distribution of juveniles may be determined by a differential larval input (see Wing et al. 1998) along the main axis of the coastal embayment. The hydrodynamic pattern of the Ria de A Coruña divides it in two parts (Montero & Prego 1997). The inner area is dominated by a clockwise eddy that may limit larval dispersion and input, depending on tidal cycle, whilst the outer zone is more influenced by oceanic circulation and can receive a greater influx of larvae. This pattern results in higher densities of juveniles in the external site, for most species, although in few cases (e.g. *Athanas nitescens*) the pattern differs, probably due to the association of the larval input with favourable tidal conditions. Nevertheless, a great range of post-settlement processes like differential mortality, dispersion and ontogenetic habitat shifts may explain the higher mesoscale homogeneity in adult distribution. However, there are some exceptions (e. g*. Pisidia longicornis*, *Porcellana platycheles*) in which adult populations could be strongly limited by juvenile distribution, i.e. by larval dispersion and settlement processes (Fernandez et al. 1990).

The major microscale variable affecting differential spatial distribution was substrate type, although some trends may be identified regarding wave exposure and depth. Some species showed slight preferences for sheltered areas where physical stress is minimized (*Processa* spp., *Pirimela denticulata*, *Porcellana platycheles*) and only species ocurring mainly in cobbles seem to prefer exposed areas. This restricted effect could be in part explained by the small variation in wave exposure at the selected spatial scale.

In general, juveniles tend to appear at deeper zones where predation risk is higher (Ruiz et al. 1993, Dittel et al. 1995) but wave disturbance is minimized. This suggests that early benthic stages are more vulnerable to physical stress while predation can be avoided by using microrefuges, available only for small individuals. Adults seem to be less vulnerable to these factors, thus occurring in a wider depth range. Generally, substrates with a complex three-dimensional structure seem to be suitable for settlement and survival of early stages of decapods (Moksnes 2002, Heck et al. 2003), while the poor structure of sandy bottoms does not fulfil the requirements of almost all taxa, as our results show. Early stages of hermit crabs are associated to this habitat because of their dependence on the use of empty gastropod shells (De Grave & Barnes

2001, Barnes & Arnold 2001) which can be found mainly in soft sediments. This behaviour allows them to avoid predation in absence of three-dimensional shelter. The strong competence for this resource among different pagurid species could lead to the complex distribution and shell use patterns observed and would explain the presence of adults in a great variety of sandy and rocky habitats.

In the study area the different rocky substrate types constitute nearby patches, among which movement may be easy for shrimps and to a lesser extent for brachyuran and anomuran crabs. Cobble substrates have been considered to play a relevant nursery role due to their abundance in a wide range of subtidal ecosystems and to their interstitial nature, which may provide shelter for a high number of species, particularly for benthic decapods (Linnane et al. 2002). The nursery function of flat rock surfaces has been less studied, but the algal communities may also provide a three-dimensional structure suitable for benthic decapods, especially for highly mobile species, as has been observed in seaweed-covered soft-bottoms (Lopez de la Rosa et al. 2002). A certain differential distribution among flat rock surfaces and cobbles was observed to be closely related to the requirements of each species, as a function of anatomical and behavioural adaptations of each group. Caridean shrimps generally seem to inhabit flat rock surfaces rather than cobbles, but the small differences in density between them may indicate a high interchange of individuals, especially for adults. Species found mostly in flat surfaces show swimming activity and cryptic adaptations to mimetize with seaweed, as in *Hyppolite* spp. Conversely, *Athanas nitescens* shows a relatively less active swimming behaviour, which may lead them to search for shelter in cobbles and crevices.

Anomuran crabs in rocky bottoms demonstrate a clear preference for cobble substrates, showing specific adaptations for inhabiting the numerous interstitial spaces present, with depressed bodies and flattened or elongated chelae. *Porcellana platycheles* occurs in the lower intertidal and upper subtidal zones restricted to shores with rocks and boulders (Stevcic 1985) as our results show. This distribution may be due to their non-territorial behaviour and reduced activity associated to microphagous feeding (Stevcic 1985). Conversely, *Pisidia longicornis* has a slight wider distribution among different

substrates although the highest abundances occur in cobbles. This is consistent with its importance in rocky bottoms along the Eastern Atlantic coast, where it appears in great variety of ecosystems, usually in cobble and gravel substrates (Robinson & Tully 2000, Sampedro et al. 1997, Linnane et al. 2002).

Variable patterns found in brachyuran crabs, with recordings of *Pilumnus* spp. and *Pirimela denticulata* on rock surfaces and *Xantho* spp. on cobbles, appear to be consistent along the whole life cycle. This may be related to their more restricted mobility respect to carideans. However, a high number of brachyuran species were found in very low densities and their ontogenic changes in distribution might differ from the patterns described above.

Focusing on kelp holdfasts, the ontogenic distribution patterns observed suggest that these habitats are used as a temporary shelter (e. g. against predation, during mating) rather than a permanent habitat or a settlement and nursery substrate. The influence of environmental stress could be attenuated inside kelp holdfasts, allowing the presence of many typically cobble-inhabiting species inside them.

Processes determining habitat use

Observed patterns of habitat use could be explained attending to the underlying processes acting at different spatial scales along the life cycle of organisms. Larval transport seems to be the main process regulating mesoscale distribution patterns of the decapods in the study area. However, microscale distribution responds to a more complex interaction among different processes, i. e. habitat selection at settlement, differential mortality among habitats, post-settlement dispersal and ontogenetic habitat shifts. There are a high number of possible combinations of these processes, but the effective number of habitat use models in natural ecosystems is more limited. We have identified here the main habitat use models in decapod species in the study area allowing to propose the possible combinations of processes originating them.

All the species showed a differential distribution among habitats, at least in juvenile stages. This can be explained by habitat selection at settlement or in early benthic stages and/or by early differential mortality. Our methodology does not allow us to discriminate between these two processes. To assess the relative importance of each mechanism it will be necessary to carry out complementary field and laboratory experiments.

Several processes may act on the patterns of spatial segregation between juveniles and adults. Ontogenetic habitat shifts are probably the major process acting on species with complete segregation or where juveniles occupy a subset of adult areas. Conversely, no migration or dispersion of adult phases would be acting in those species with no spatial segregation. Small scale dispersion movements can result in a more extended distribution of adults but without a real juvenile/adult disjunction. Differential mortality will interact with these processes creating more complex patterns where the individual effect of each process is difficult to discriminate.

Determining the nursery role of these shallow habitats will require more accurate studies focused on identifying local areas that fulfil the requirements to be considered as main nursery grounds, taking into account the larval input, juvenile survival and growth and the resulting contribution to adult populations.

Acknowledgements: Financial support for this study was given by the Consellería de Educación e Ordenación Universitaria of the Xunta de Galicia (grant XUGA10301B97) and the Spanish Ministerio de Ciencia y Tecnología (grants DIMEPIC, REN2000 – 0446MAR, and ECOSOST, REN2003-04816). The authors would like to thank P. Sampedro, who helped in the field work, and E. Godinez-Dominguez for his assistance in data analyses.

LITERATURE CITED

Abele LG (1982) Biogeography. In: Bliss DG, Abele LG (eds) The Biology of Crustacea, Vol. 1: Systematics, the Fossil Record, and Biogeography. New York, Academic Press.

Barnes DKA, Arnold RJ (2001) Ecology of subtropical hermit crabs in SW Madagascar: cluster structure and function. Mar Biol 139: 463-474

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51: 633-641

Benvenuto C, Gherardi F (2001) Population structure and shell use in hermit crab, *Clibanarius erithropus*: a comparison between Mediterranean and Atlantic shores. J Mar Biol Ass UK 81: 77-84

Bertini G, Fransozo A (1999) Relative growth of *Petrochirus diogenes* (Linnaeus, 1758) (Crustacea, Anomura, Diogenidae) in the Ubatuba Region, Sao Paulo, Brazil. Rev Bras Biol 59: 617-625

Caddy, JF (ed) (1989) Marine invertebrate fisheries: their assessment and management. 1998. New York, John Wiley & Sons

Cosme de Avilés A, Prego R (1995) Características generales de la Ría de La Coruña y su cuenca fluvial. Monografías de Química Oceanográfica 2: 25-45

De Grave S, Barnes DKA (2001) Ecology of tropical hermit crabs (Crustacea Decapada) at Quirimba Island, Mozambique: a mulitvariate assemblage perspective. Tropical Zoology 14: 197-209

Dittel AI, Hines AH, Ruiz GM, Ruffin KK (1995) Effects of shallow water refuge on behaviour and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. Bull Mar Sci 57: 902-916

Fariña AC, Freire J, Gonzalez-Gurriaran E (1997) Megabenthic decapod crustacean assemblages on the Galician continental shelf and upper slope. Mar Biol 127: 419-434

Fernandez L, Gonzalez-Gurriaran E, Freire J, Muiño R (1990) Abundancia y distribución de Pisidia longicornis (Linnaeus, 1767) (Decapoda, Anomura) en relación con la dinámica del cultivo de mejillón en la Ría de Arousa (Galicia, NW España) (Abundance and distribution of Pisidia longicornis (Linnaeus, 1767) (Decapoda, Anomura) related to mussel culture dynamics in the Ria de Arousa (Galicia, NW Spain) Bol R Soc Esp Hist Nat (Sec Biol) 86:181-193

Freire J, Bernardez C, Corgos A, Fernandez L, Gonzalez-Gurriaran E, Sampedro MP, Verísimo P (2002) Management strategies for sustainable invertebrate fisheries in coastal ecosystems of Galicia (NW Spain) Aquat Ecol 36: 41-50

Freire J, Carabel S, Verísimo P, Bernardez C, Fernandez L (submitted) Complex patterns of habitat use by juvenile spider crabs Maja brachydactila revealed by stable isotope analyses (2005) Mar Ecol Prog Ser (submitted)

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine invertebrates. Mar Ecol Prog Ser 247: 281-295

Gonzalez-Gurriaran E, Freire J, Bernardez C (2002) Migratory patterns of female spider crabs *Maja squinado* detected using electronic tags and telemetry. J Crust Biol 22: 91-97

González-Gurriaran E, Mendez M (1986) Crustáceos decápodos das costas de Galicia. I. Brachyura. Cuadernos da Área de Ciencias Biológicas, Seminario de Estudos Galegos, Vol. 2 (2nd edn). A Coruña, Ediciones do Castro.

Hayward PJ, Isaac MJ, Makings P, Moyse J, Naylor E, Smaldon G (1995) Crustaceans (Phylum Crustacea). In: Hayward PJ & Ryland JS (eds) Handbook of the Marine Fauna of North-West Europe. Oxford, Oxford University Press.

Heck Jr. KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253: 123-136

Ingle RW (1996) Shallow-water crabs. In: Barnes RSK, Crothers JH (eds) Synopses of the British Fauna No. 25. London, The Linnean Society of London and The Estuarine and Coastal Sciences Association.

Linnane A, Ball B, Munday B, Browne R, Mercer JP (2002) Faunal description of an Irish cobble site using airlift suction sampling. Biology and Environment: Proceedings of the Royal Irish Academy 103: 41-48

Lopez de la Rosa I, Garcia Raso JE, Rodriguez A (2002) Evolution of a decapod community (Crustacea) of shallow soft bottoms with seaweeds from southern Europe. J Mar Biol Ass UK 82: 85-95

Moksnes PO, Hedvall O, Reinwald T (2003) Settlemet behaviour in shore crabs *Carcinus maenas*: why do postlarvae emigrate from nursery habitats? Mar Ecol Prog Ser 250: 215-230

Moksnes PO (2004) Interference competition for space in nursery habitats: density-dependent effects on growth and dispersal in juvenile shore crabs *Carcinus maenas*. Mar Ecol Prog Ser 281: 181-191

Montero P, Prego R, Gomez-Gesteira M, Neves R, Taboada JJ, Perez-Villar V (1997) Aplicación de un modelo 2D al transporte de partículas en la Bahía de A Coruña. In: Procesos biogeoquímicos en sistemas costeros hispano-lusos. Prego R, Fernandez JM (eds) Pontevedra, Excma Diputación Provincial de Pontevedra.

Oh CW, Hartnoll RG (1999) Size at sexual maturity, reproductive output, and seasonal reproduction of *Philocheras trispinosus* (Decapoda) in Port Erin Bay, Isle of Man. J Crust Biol 18: 252-259

Orensanz JM, Jamieson GS (1998) The analysis of concentration and crowding in shellfish research. In: Jamieson GS, Campbell A (eds) Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can Spec Publ Fish Aquat Sci 125: 143-157

Palma AT, Steneck RS, Wilson CJ (1999) Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. J Exp Mar Biol Ecol 241: 107-136

Paula J, Dray T, Queiroga H (2001) Interaction of offshore and inshore processes controlling settlement af brachyuran megalopae in Saco mangrove creek, Inhaca Island (South Mozambique). Mar Ecol Prog Ser 215: 251-260

Pfister CA (1997) Demographic consequences of within-year variation in recruitment. Mar Ecol Prog Ser 153: 229-238

Pile AJ, Lipcius RJ, Van Montfrans J, Orth RJ (1996) Density-dependent settler-recruit-juvenile relationships in blue crabs. Ecol Monogr 66: 277-300

Robinson M, Tully O (2000) Spatial variability in decapod community structure and recruitment in subtidal habitats. Mar Ecol Prog Ser 194: 133-141

Roughgarden J, Gaines JS, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar Ecol Prog Ser 99: 1-16

Sampedro MP, Fernandez L, Freire J, Gonzalez-Gurriaran E (1997) Fecundity and reproductive output of *Pisidia longicornis* (Decapoda, Anomura) in the Ria de Arousa (Galicia, NW Spain). Crustaceana 70: 95-110

Squires HJ (1990) Decapod crustacea of the Atlantic coast of Canada. Can Bull Fish Aquat Sci 221: 532 pp

Squires HJ, Ennis GP, Dawe G (2000) On biology of the shrimp *Eualus pusiolus* (Kroyer, 1841) (Crustacea, Decapoda) at St. Chad's, Newfoundland. Sci Counc Stud Nafo 33: 1-10

Stevcic Z (1985) Autoecological investigations of the porcelain crab *Porcellana platycheles* (Pennant) (Decapoda, Anomura) in the Rovijn area (Northern Adriatic). Crustaceana 55: 242-252

Stoner (2003) What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. Mar Ecol Prog Ser 257: 275-289

Van Montfrans J, Ryer CH, Orth RJ (2003) Substrate selection by blue crab *Callnectes sapidus* megalopae and first juvenile instars. Mar Ecol Prog Ser 260:209-217

Williams AB (1984) Shrimps, lobsters and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Washington, Smithsonian Institution Press.

Wing SR, Botsford LW, Quinn JF (1998) The impact of coastal circulation on the spatial distribution of invertebrate recruitment, with implications for management. In: Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Jamieson GS, Campbell A (eds) Can Spec Publ Fish Aquat Sci 125: 285-294

Zariquiey Álvarez R (1968) Crustáceos decápodos ibéricos. Investigación pesquera, 32. Consejo Superior de Investigaciones Científicas, Barcelona.

FIGURE LEGENDS

Figure 1. Ria de A Coruña, NW Spain. Sampling sites located along its eastern coastline: Portocobo (PC), Canide (CE) and Canabal (CL).

Figure 2. Size frequency distribution of decapod crustaceans found in the samples. A) Caridea, B) Anomura, C) Brachyura. Note different size ranges in Brachyura.

Figure 3. Densities of taxa found in each depth strata on sandy substrate. Note scale breaks in the density axis.

Figure 4. Mean densities of juvenile (white boxes) and adult (black boxes) caridean taxa in flat rock surface, cobble and kelp holdfast samples for each class of the other environmental variables (sampling station, wave exposure level, and depth). Densities are calculated as individuals·m^{-2} for the first two substrates and as individuals per holdfast for the latter. Boxes and whiskers represent the standard error and 95% confidence interval, respectively. Ex= exposed, Sh=sheltered.

Figure 5. Mean densities of juvenile (white boxes) and adult (black boxes) brachyuran taxa in flat rock surface, cobble and kelp holdfast samples for each class of the other environmental variables (sampling station, wave exposure level, and depth). Densities are calculated as individuals·m^{-2} for the first two substrates and as individuals per holdfast for the latter. Boxes and whiskers represent the standard error and 95% confidence interval, respectively. Ex= exposed, Sh=sheltered.

Figure 6. Mean densities of juvenile (white boxes) and adult (black boxes) anomurans in flat rock surface, cobble and kelp holdfast samples for each level of the other environmental variables (sampling station, wave exposure and depth). Densities are calculated as individuals·m^{-2} for the first two substrates and as individuals per holdfast for the latter. Boxes and whiskers represent the standard error and 95% confidence interval, respectively. Ex= exposed, Sh=sheltered.

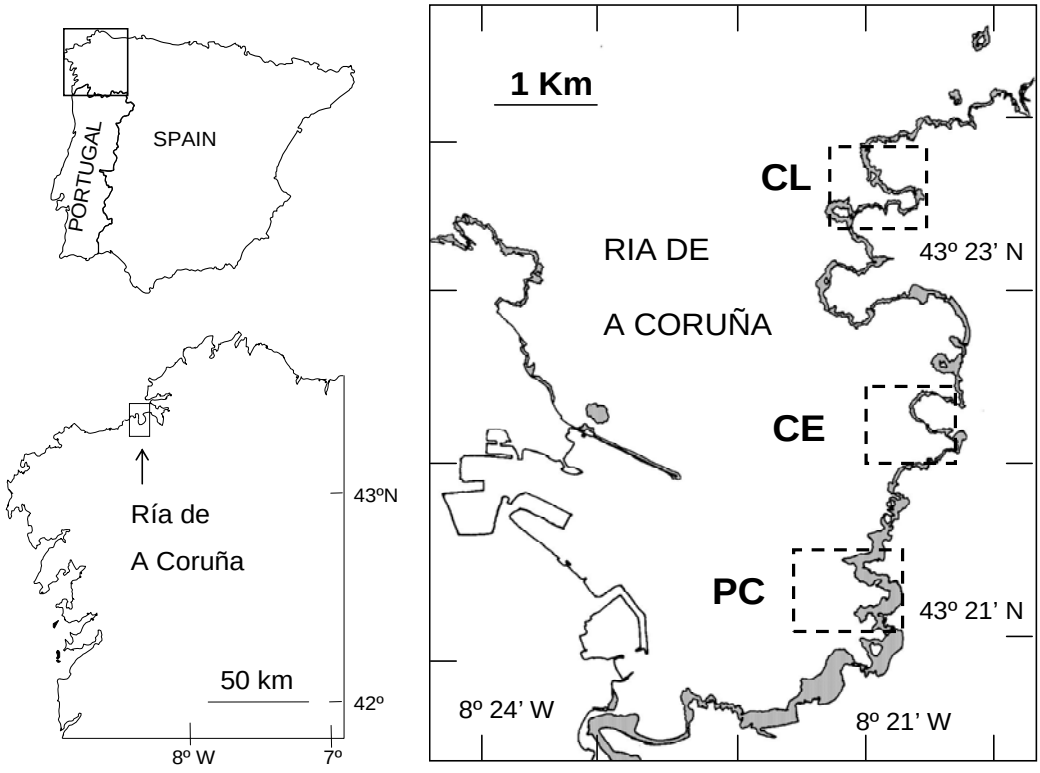

Fig. 1. Pallas et al.

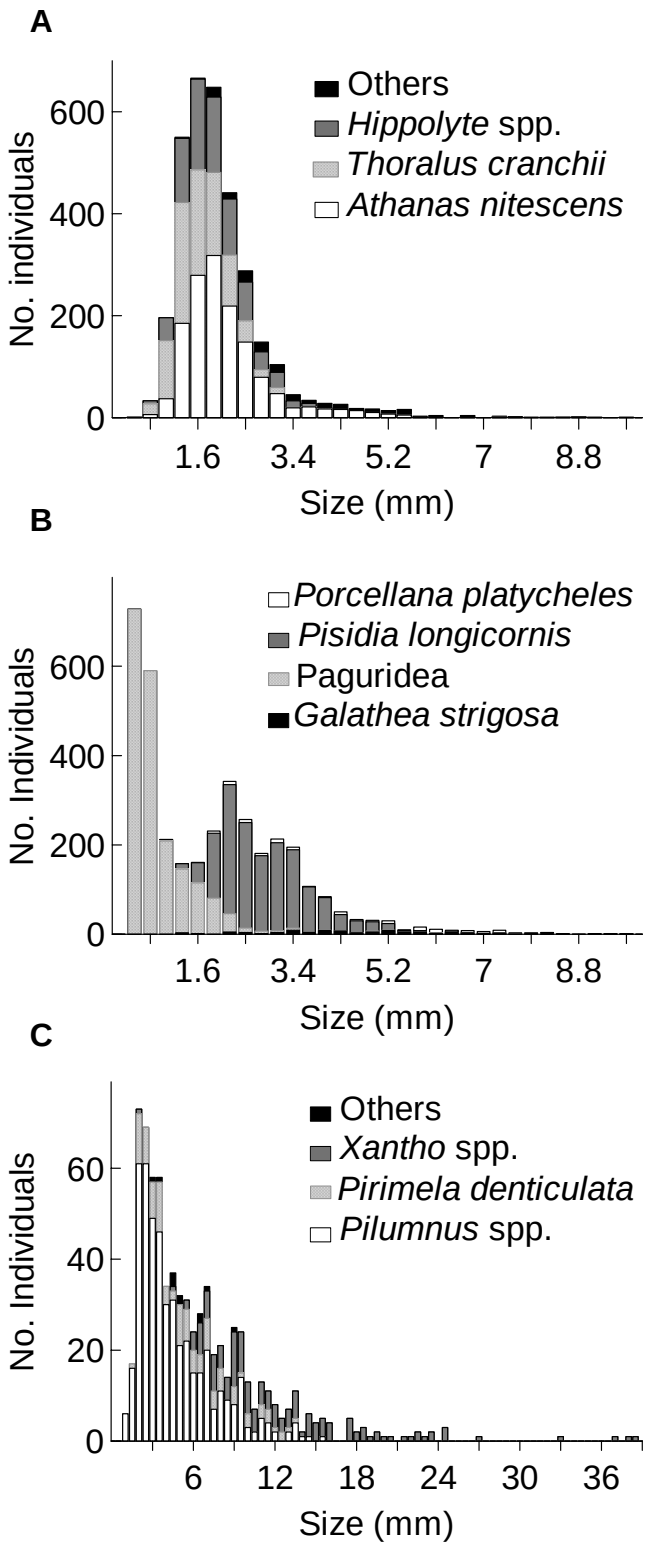

Fig. 2. Pallas et al.

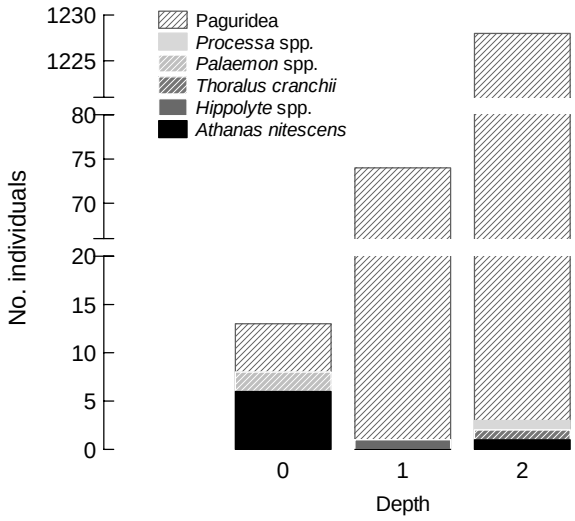

Fig. 3. Pallas et al.

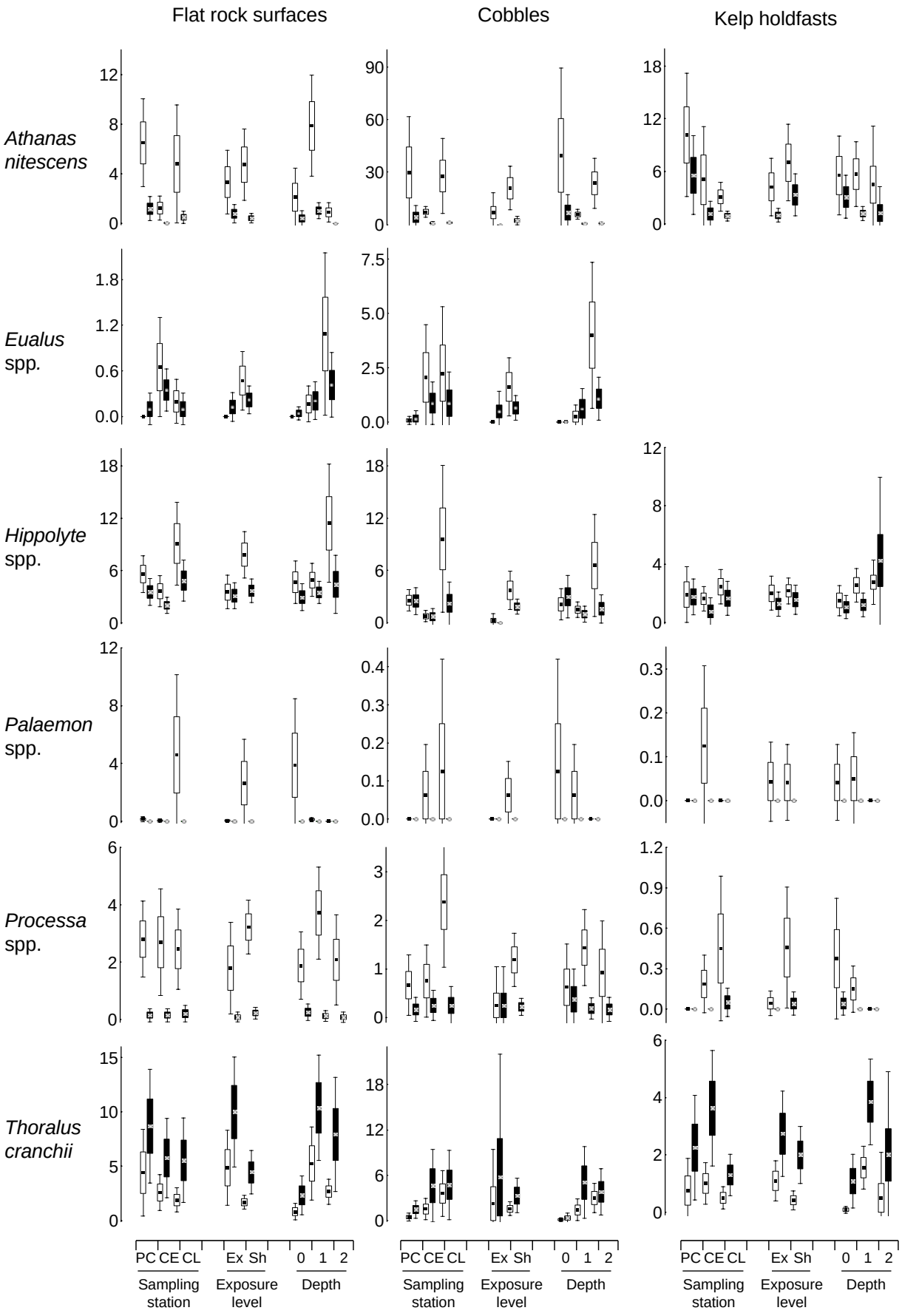

Fig. 4. Pallas et al.

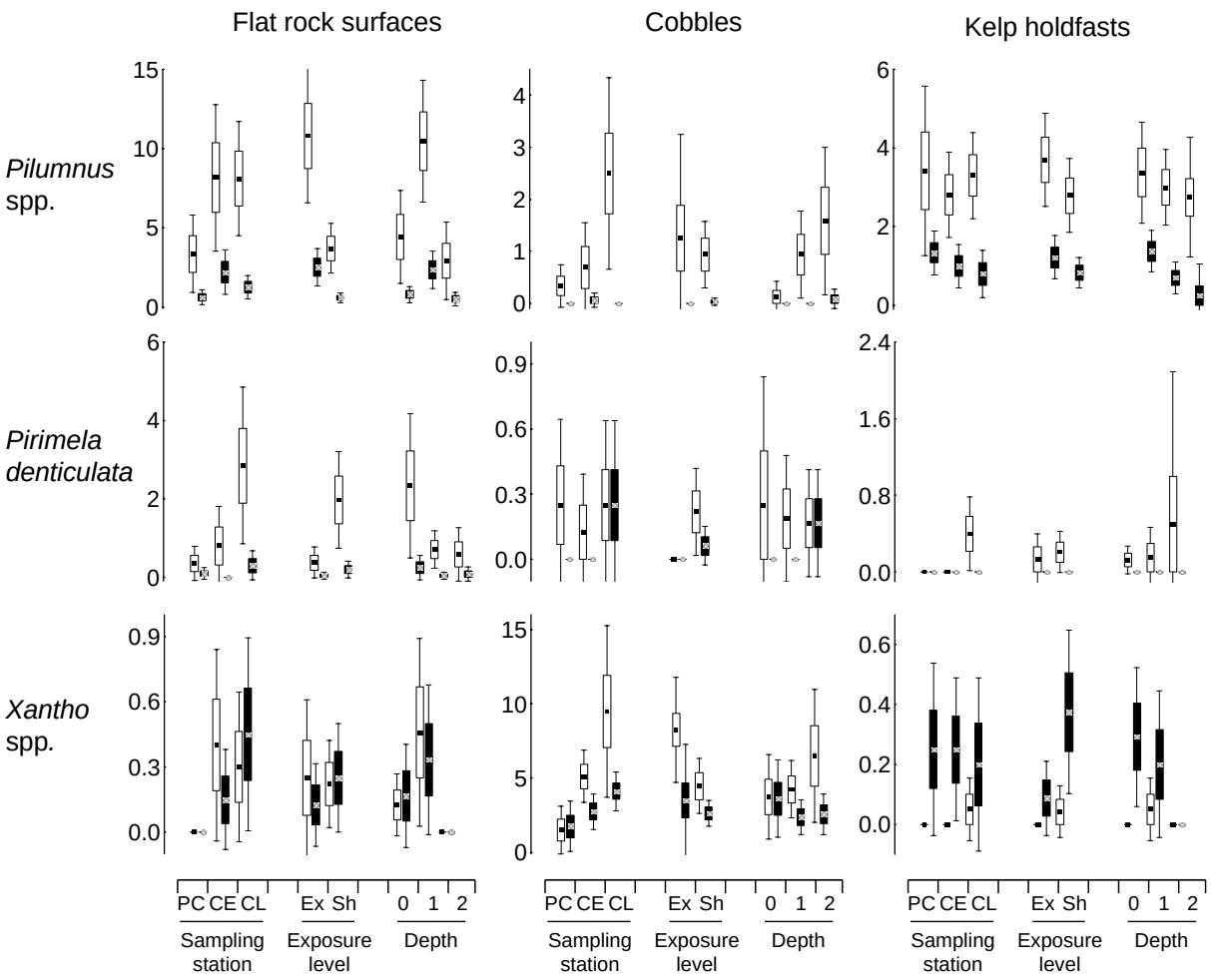

Fig. 5. Pallas et al.

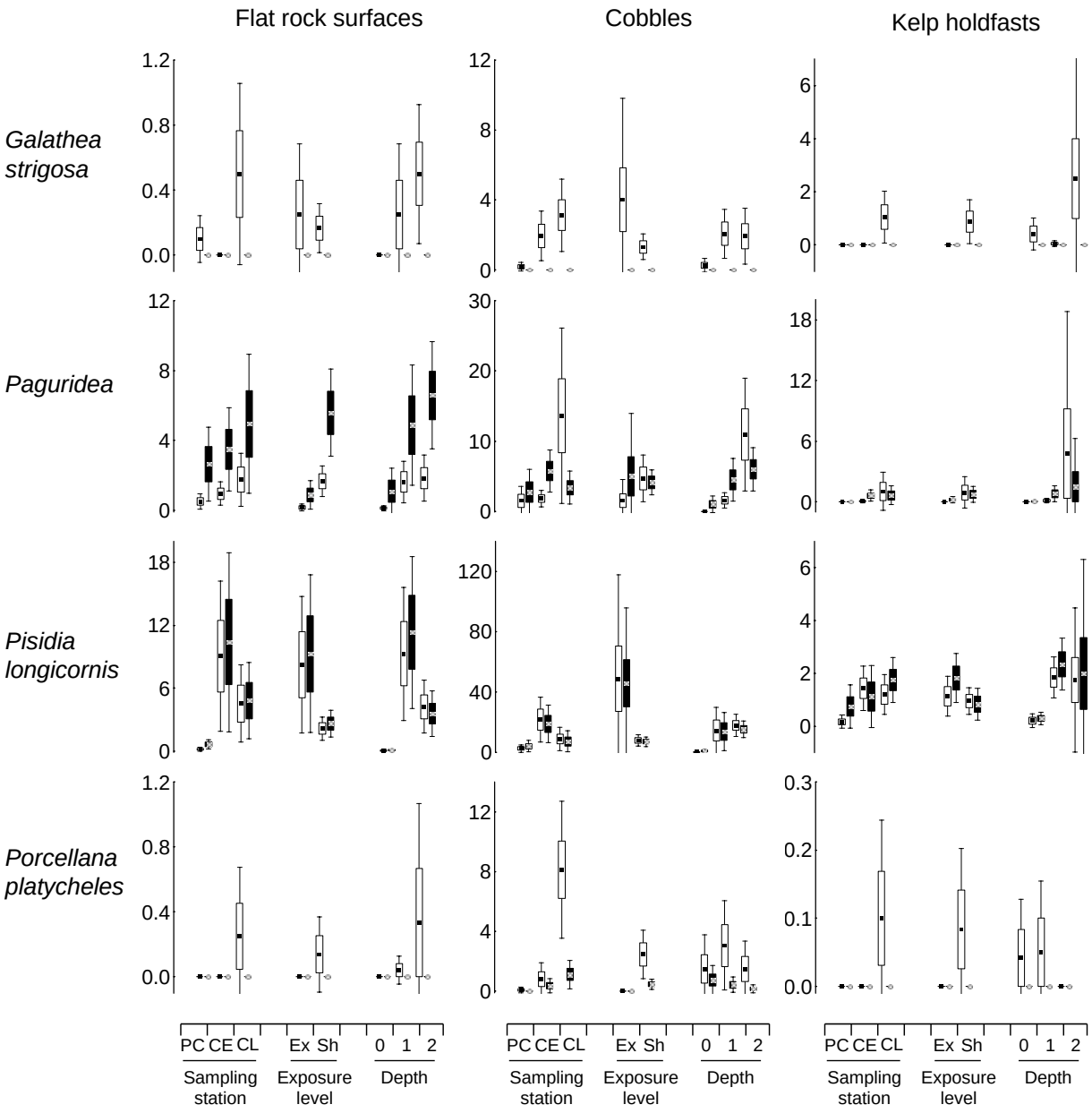

Fig. 6. Pallas et al.

Table 1. Abundances, mean densities and adult/juvenile ratios of decapod crustacean taxa found in shallow benthic habitats of the Ria de A Coruña. The taxa in bold (relative abundance >1%) were used in the analyses. Species pooled as genera due to identification difficulties: *Hippolyte* (represented by the species *H. varians* and *H. longirostris*), *Pilumnus* (*P. hirtellus, P. spinifer*), *Xantho* (*X. incisus, X. pilipes*), *Processa* (*P. edulis, P. modica*), *Eualus* (*E. occultus, E. pusiolus*), *Palaemon* (*P. longirostris*, *P. serratus*, *P. elegans*), *Philocheras* (*P. fasciatus*, *P. trispinosus*) and *Liocarcinus* (*L. arcuatus*, *L. vernalis*). Sexual maturity criteria: I) Size of smallest ovigerous female, II) Size of maturity in literature.

					Mean densities			
Taxon	**Nº ind**	**Relative abundance (%)**	**Sexual maturity (mm)**	**criteria**	**Sandy bottoms (nº ind m^{-2})**	**Rocky bottoms (nº ind m^{-2})**	**Kelp holdfasts (nº ind/holdfast)**	**Proportion of adults**
Caridea								
Athanas nitescens	**1432**	**16.19**	**2.8**	**I**	**2.33**	**44.04**	**7.67**	**0.15**
***Hippolyte* spp.**	**936**	**10.58**	**1.7**	**I**	**0.33**	**31.96**	**3.50**	**0.36**
Thoralus cranchii	**929**	**10.51**	**1.4**	**I**	**0.33**	**32.54**	**3.06**	**0.70**
***Processa* spp.**	**230**	**2.60**	**5.8**	**I**	**0.33**	**9**	**0.27**	**0.08**
***Eualus* spp.**	**105**	**1.19**	**1.8**	**I**	**0**	**4.38**	**0**	**0.33**
***Palaemon* spp.**	**102**	**1.15**	**10**	**II**	**0.67**	**4.08**	**0.04**	**0**
Philocheras spp.	53	0.60	3.5	I	2	1.88	0.04	0.02
Alpheus macrocheles	28	0.32	4.5	I	0	1.17	0	0.29
Brachyura								
***Pilumnus* spp.**	**713**	**8.06**	**7**	**II**	**0**	**21.38**	**4.17**	**0.18**
***Xantho* spp.**	**316**	**3.57**	**9**	**II**	**0**	**12.63**	**0.27**	**0.39**
Pirimela denticulata	**106**	**1.20**	**11.3**	**I**	**0**	**4.08**	**0.17**	**0.10**
Necora puber	49	0.55	49.8	II	0	1.67	0.19	0
Inachus phalangium	13	0.15	9.8	II	0	0.38	0.08	0.54
Macropodia rostrata	11	0.12	13.9	I	0	0.46	0	0.09
Liocarcinus spp.	8	0.09	25	II	0.67	0.25	0	0
Pisa tetraodon	7	0.08	21.2	II	0	0.29	0	0.29
Cancer pagurus	5	0.06	127	II	0	0.17	0.02	0
Achaeus gracilis	4	0.05	5.8	II	0	0.17	0	0.75
Achaeus cranchii	3	0.03	5.8	II	0	0.13	0	0.67
Maja brachydactila	3	0.03	120	II	0	0.13	0	0
Ebalia tuberosa	2	0.02	-	-	0	0.08	0	-
Eurynome aspera	2	0.02	8	II	0	0.08	0	0
Anomura								
Paguridea	**1942**	**21.96**	**1.2**	**I**	**434.33**	**24.75**	**0.94**	**0.21**
Pisidia longicornis	**1568**	**17.73**	**2.8**	**I**	**0**	**60.71**	**2.31**	**0.50**
Porcellana platycheles	**102**	**1.15**	**7**	**I**	**0**	**4.17**	**0.04**	**0.15**
Galathea strigosa	**92**	**1.04**	**34.6**	**II**	**0**	**2.96**	**0.44**	**0**
Unidentified	82	0.93	-	-	0	2.96	0.23	-
Total	8843				441	266.46	23.44	0.32

Table 2. Results of GLM fitted to the distribution of the most abundant species of decapod crustaceans in shallow rocky bottoms in the Ria de A Coruña. Values estimated for the different levels of the variables are relative to the missing level of each one, considered as 0 level. Variables included in the most parsimonious models are indicated with asterisks. Percentage of models in which a variable has been included is showed. P-values showed indicate the significance of the most parsimonious model for each species.

		Mesoscale (kms)			(100s m)		Microscale (10s m)			(m)		
		Sampling station			Wave exposure		Depth			Microhabitat		
Species	Intercept		Canide	Canabal		Sheltered		Depth 0	Depth 1		Cobbles	p
Juveniles												
Caridea												
Athanas nitescens	12.00	*	-7.33	2.77		1.20		3.67	-2.76	*	8.24	<0,001
Eualus spp.	0.98	*	0.59	0.08		0.01	*	-0.78	-0.77	*	0.39	<0,001
Hippolyte spp.	4.85	*	-2.51	3.46	*	1.06	*	-1.49	-1.60	*	-1.67	<0,001
Palaemon spp.	0.36	*	-0.93	2.21	*	1.29	*	2.20	-0.56		-0.65	0.004
Processa spp.	1.28		-0.07	0.15	*	0.91	*	-0.45	1.14	*	-1.05	<0,001
Thoralus cranchii	3.06		-0.39	-0.33	*	-1.59	*	-2.30	0.92		-0.50	<0,001
Brachyura												
Pilumnus spp.	4.92	*	0.36	1.55	*	-2.66	*	-1.79	1.80	*	-2.14	<0,001
Pirimela denticulata	0.43	*	-0.34	1.11	*	0.81	*	1.04	-0.17	*	-0.57	<0,001
Xantho spp.	2.99	*	0.11	1.30		-0.57		-0.41	-0.42	*	2.48	<0,001
Anomura												
Galathea strigosa	1.14	*	-0.02	0.60	*	-0.38	*	-0.52	0.07	*	0.77	<0,001
Paguridae	3.16	*	-1.20	2.75		0.06	*	-2.00	-1.16	*	1.47	<0,001
Pisidia longicornis	11.70	*	6.40	-1.20	*	-7.14	*	-7.79	1.31	*	4.38	<0,001
Porcellana platycheles	1.02	*	-0.77	1.73		0.39		0.03	0.46	*	1.11	<0,001
%		84.6			61.5		76.9			84.6		
Adults												
Caridea												
Athanas nitescens	1.22	*	-0.89	-0.22		0.20	*	1.21	-0.17	*	0.88	0.026
Eualus spp.	0.41		0.23	-0.02		0.00	*	-0.30	-0.03	*	0.16	0.017
Hippolyte spp.	2.59	*	-1.31	1.07		0.24		0.02	-0.18	*	-0.86	<0,001
Processa spp.	0.16		0.01	0.04	*	0.07		0.12	-0.02		0.03	0.317
Thoralus cranchii	6.35		-0.30	-0.72	*	-2.81	*	-4.56	2.23	*	-1.35	<0,001
Brachyura												
Pilumnus spp.	0.95	*	0.42	-0.06	*	-0.69	*	-0.46	0.43	*	-0.54	<0,001
Pirimela denticulata	0.09	*	-0.11	0.17		0.06		0.09	-0.07		-0.03	0.018
Xantho spp.	1.49	*	-0.06	0.59		0.00		0.28	-0.07	*	1.34	<0,001
Anomura												
Paguridae	3.07		0.86	0.30	*	1.65	*	-2.69	1.12		-0.62	<0,001
Pisidia longicornis	11.12	*	5.93	-1.60	*	-6.78	*	-7.61	2.61	*	3.46	<0,001
Porcellana platycheles	0.17	*	-0.03	0.21		0.09		0.13	0.04	*	0.22	<0,001
%		63.6			45.4		54.5			72.7		

Table 3. Results of GLM fitted to the distribution of the most abundant species of decapod crustaceans in kelp holdfasts in the Ria de A Coruña. Values estimated for the different levels of the variables are relative to the missing level of each one, considered as 0 level. Variables included in the most parsimonious models are indicated with asterisks. Percentage of models in which a variable has been included is showed. P-values showed indicate the significance of the most parsimonious model for each species.

		Mesoscale (kms)			(100s m)		Microscale (10s m)			
		Sampling station			Wave exposure		Depth			
Species	Intercept		Canide	Canabal		Sheltered		Depth 0	Depth 1	p
Juveniles										
Caridea										
Athanas nitescens	6.15	*	-1.27	-3.59	*	-2.29		-0.61	0.98	0.05
Hippolyte spp.	2.13		-0.42	0.33		-0.13	*	-0.63	0.47	0.27
Palaemon spp.	0.04	*	0.08	-0.04		0.00		0.00	0.00	0.11
Processa spp.	0.00		-0.07	0.30	*	-0.22		0.37	0.15	0.06
Thoralus cranchii	0.88		0.20	-0.30	*	0.24	*	-0.80	0.64	<0,001
Brachyura										
Pilumnus spp.	3.05		-0.34	0.28	*	0.39		0.32	-0.12	0.29
Pirimela denticulata	0.17	*	-0.13	0.25		0.00		-0.04	-0.04	0.04
Xantho spp.	0.00		-0.03	0.04	*	-0.03		0.00	0.06	0.31
Anomura										
Galathea strigosa	0.76		-0.24	0.45		-0.24	*	-0.34	-0.71	0.00
Paguridae	1.60		-0.02	0.04		-0.08	*	-1.60	-1.43	<0,001
Pisidia longicornis	1.23	*	0.48	0.10		0.13	*	-1.02	0.48	<0,001
Porcellana platycheles	-0.01		-0.05	0.08	*	-0.05		0.05	0.06	0.14
%		33.3			50		41.6			
Adults										
Caridea										
Athanas nitescens	0.72592	*	0.7206	0.7206	*	0.52625		0.82976	0.85712	<0,001
Hippolyte spp.	0.40		0.40	0.40		0.29	*	0.46	0.47	0.01
Processa spp.	0.03		0.03	0.03	*	0.02		0.03	0.03	0.31
Thoralus cranchii	0.50	*	0.50	0.50		0.36	*	0.57	0.59	0.00
Brachyura										
Pilumnus spp.	0.22		0.21	0.21		0.16	*	0.25	0.25	0.04
Xantho spp.	0.10		0.10	0.10	*	0.07		0.12	0.12	0.04
Anomura										
Paguridae	0.28		0.28	0.28		0.20	*	0.32	0.33	0.06
Pisidia longicornis	0.31		0.30	0.30	*	0.22	*	0.35	0.36	<0,001
%		25			50		62.5			